

FIRE-DEPENDENT REPRODUCTIVE STRATEGIES

IN ARCTOSTAPHYLOS AND CEANOTHUS ^{1/}

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Abstract: The question is addressed "why have the majority of Arctostaphylos and Ceanothus species apparently (through evolutionary time) lost the ability to resprout after fire." It is proposed that loss of the sprout-producing burl was adaptive in an environment which put a premium on seedling establishment over sprouting. The hypothesis is offered that this environment was one in which there were (occasionally) long fire-free periods. This was tested by comparing regional and elevational patterns of lightning fires with patterns of abundance and diversity of nonsprouting and sprouting Arctostaphylos and Ceanothus.

Key words: Arctostaphylos; Ceanothus; lightning; fire; reproductive strategies.

INTRODUCTION

Wildfires are frequent in the California chaparral. The reasons are 1) man provides a ready source of ignition, 2) the Mediterranean-climate summer drought produces a very flammable vegetation, and 3) the dense nature of the vegetation results in a very rapid and extensive fire spread. Even though man has been a part of this ecosystem for a relatively brief 15,000 yrs (Martin 1973) it is almost unquestionable that fire has been an important selective force in this system for a much longer time. This is based on a number of observations. One is that the mediterranean climate, and consequently the flammability characteristics of the vegetation date back to at least the Pliocene epoch 10 million yrs ago (Axelrod 1973). A second is that lightning presently is a natural source of fire and there is little reason to suspect it hasn't also been in the past. Thirdly, chaparral shrubs have several specialized struct-

ural adaptations which provide for their rapid reestablishment after fire. For example, seeds which remain dormant in the soil until stimulated by fire and basal burls which send up a proliferation of new shoots. These observations make it reasonable to assume that fire has been a major evolutionary force in this vegetation.

From a fire-management point of view an understanding of the dynamics of shrub reestablishment after fire is vitally important and this is dependent upon an understanding of the reproductive strategies evolved by these shrubs.

As mentioned, shrubs reestablish after fire by seedlings and/or resprouts from belowground vegetative parts (not all resprouting species possess burls). The dependence upon seedlings or resprouts varies from species to species as well as from population to population within a species. Schematically we can picture a species' reproductive tactic falling somewhere along the abscissa of the graph in figure 1. However, this position will vary spatially (from population to population) and temporally (from one fire to the next). A species is then best characterized as having a reproductive strategy which occupies a region along the abscissa (see Keeley and Zedler 1977). Thus, since Quercus sp. for example resprout but establish very few seedlings after fire they would occupy the region (a) farthest to the left. Proceeding to the right we pick up Prunus sp.,

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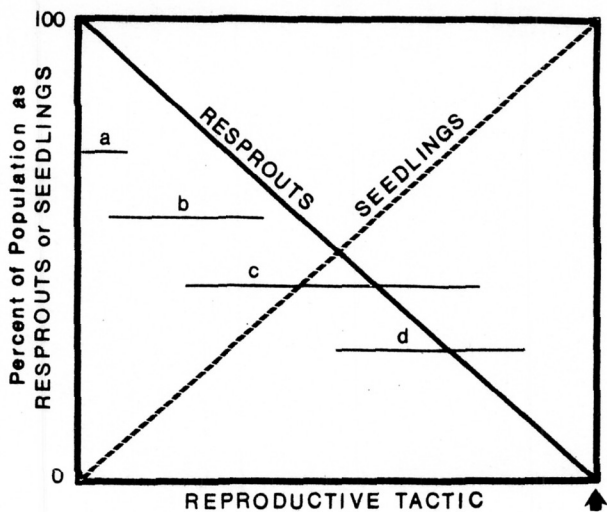


Figure 1--Reproductive options available to chaparral shrubs.

Rhamnus sp., Heteromeles arbutifolia, Rhus ovata, certain Arctostaphylos sp. and Cercocarpus sp. (region b), and the nearly ubiquitous Adenostoma fasciculatum would likely occupy the broadest region perhaps around the middle of the axes (c) followed by certain Ceanothus sp. to the right of center (d). There is however one group of species which form a significant exception to this pattern. The majority of Arctostaphylos and Ceanothus species do not occupy a region along the abscissa but rather a single point. These species are totally incapable of resprouting under any condition and thus are entirely dependent upon seedling production for post-fire regeneration. They are obligate-seeders.

We can therefore define two groups of species; those that resprout after fire and those that don't. Resprouters occupy a region along the reproductive tactic axes, the position being determined by the individual species' resistance to fire and the intensity of the fire both of which will be affected by a multitude of factors such as age of the shrubs, density of the vegetation, season of the fire, weather patterns prior to, during, and after the fire, being very important. Nonsprouters can operationally be defined as incapable of resprouting under any condition in which the tops are removed, by fire or any other means. It is this group of shrubs composed entirely of Arctostaphylos and Ceanothus species which I will focus on in this paper.

The very different response to fire of sprouters and obligate-seeders raises some questions. It would seem that a long-lived species with the ability to survive fires and resprout vigorously should have a tremendous

competitive advantage. Once such a species had appropriated space it would occupy it for a long time. After fire, the well-developed root system should allow for a greater allocation of resources to aboveground growth thus making it almost immune from serious competition for some yrs. In addition these resprouts are capable of heavy seed production within the second yr after fire whereas seedlings may require upwards of 10 yrs before a significant seed crop is produced.

In contrast, the obligate seeding life-history seems less obviously advantageous. Since all of the shrubs die in the fire and no significant seed germination takes place except after fires, species with this life-history are dependent upon accumulating seeds in the soil. This would suggest allocation of a large proportion of energy to annual seed production. But some balance must be struck between growth and reproduction. Too much allocation to growth would be risky should the interval between fires occasionally be relatively short. It seems that a species that loses completely the ability to resprout would be in a far more precarious position than one which could sprout to at least some extent.

Evidence based mainly on systematic considerations is quite convincing that the obligate seeding species of Arctostaphylos and Ceanothus were derived from sprouting ancestors, i.e., evolutionarily they have lost the ability to resprout (Wells 1969, Stebbins 1974, p. 192). This, coupled with the fact that the majority of species in these two genera (the largest shrubby genera in the chaparral) are obligate-seeders and they form a very significant part of the chaparral community suggests there must be an adaptive advantage to reestablishing entirely by seedlings.

HYPOTHESES

Two hypothetical advantages to be gained by not producing a burl are:

- 1) a genetic advantage
- 2) an ecological advantage

A genetic advantage could arise as follows. Under conditions of recurring fire the loss of the burl would mean a greater number of sexual generations resulting in a greater frequency of natural selection (Wells 1969). This implies that obligate-seeding species are capable of a closer and more rapid adjustment to the environment than resprouting species (Raven 1973). Thus by establishing each new generation with

^{3/} Personal observations.

sexually produced progeny nonsprouting species gain some sort of evolutionary advantage over already established individuals.

This hypothesis is not overly compelling. One reason is that nonsprouters do not appear to have any such obvious advantage; sprouting species are very successful. That is, sprouters and seeders coexist so we simply can't explain the advantage of one group at the expense of the other. A second reason is that the sprouting species of *Arctostaphylos* and *Ceanothus* also produce many seedlings. The genetic hypothesis argues that these sprouting forms could gain an advantage by not sprouting in that there would be greater space and resources for their seedlings and consequently more seedlings would establish and consequently there would be greater genetic variation for natural selection to act on. However, this advantage must necessarily be shared with seedlings of all other species. It is certainly questionable whether or not the small increase in seedling number and the consequently slight increase in genetic variability are sufficient to cause complete loss of the burl.

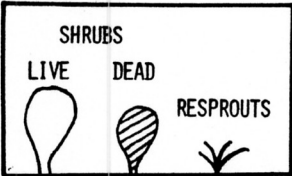
The ecological hypothesis argues that the obligate-seeders evolved in an environment which favored the establishment of seedlings and concomitantly put less of a premium on resprouting. A corollary to this may be that the complete loss of the burl was of selective value because of the energetic gain to accrue by no longer allocating energy to burl production or maintenance.

What sort of environment was it? First, seedlings do not establish in mature chaparral; they are adapted to openings. Secondly, openings generally occur only after fires. Thirdly, in the postfire environment seedlings stand very little chance in close competition with resprouts. Therefore, situations which result in the fewest resprouts after a fire will produce the optimum environment for seedlings.

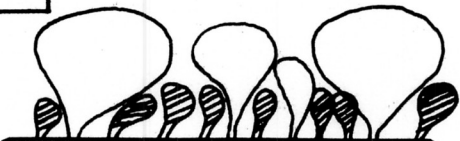
Based on these observations one could hypothesize a number of such situations. While acknowledging that there is no compelling evidence for accepting any one answer I would like to propose one such hypothesis.

PREFIRE ASPECT

25 years



100 years



POSTFIRE ASPECT



SHORT FIRE CYCLE

- 1. FEWER DEAD SHRUBS PRIOR TO THE FIRE
THUS, MORE POTENTIAL RESPROUTS
- 2. LESS INTENSE FIRES
THUS, LOWER MORTALITY OF
SPROUTING SHRUBS
- THE RESULT IS SMALLER OPENINGS
FOR SEEDLINGS
- CONCLUSION: LOW SELECTION PRESSURE
FOR OBLIGATE-SEEDING



LONG FIRE CYCLE

- 1. MORE DEAD SHRUBS PRIOR TO THE FIRE
THUS, FEWER POTENTIAL RESPROUTS
- 2. MORE INTENSE FIRES
THUS, HIGHER MORTALITY OF
SPROUTING SHRUBS
- THE RESULT IS LARGER OPENINGS
FOR SEEDLINGS
- CONCLUSION: HIGH SELECTION PRESSURE
FOR OBLIGATE-SEEDING

Figure 2--Model of the relationship between successional changes in the density of live shrubs and relative abundance of postfire resprouting shrubs resulting from fires early vs. late in succession.

For want of a better name I shall call this the "Stochastic-Fire Hypothesis." If we consider a prehistoric chaparral environment composed entirely of sprouting species then the size of postfire openings will be highly dependent upon the frequency and intensity of fires in the environment.

In this pre-hominid environment lightning is the only significant source of fires and these fires are randomly distributed both in time and space. The result is that any given area of chaparral has a high probability of an occasional short period of time between fires and an occasional long period of time between fires. Since obligate-seeders depend upon building up seed pools in the soil the shorter the period between fires the greater the advantage is to sprouters. However, occasional extended periods of time between fires should work the other way, i.e., favor seeders over sprouters.

There are several reasons for this. Seeds of chaparral shrubs are adapted to surviving very long periods of dormancy. In fact there is little difference in the number of seedlings after fires in 100-yr-old and 20-yr-old chaparral (Keeley and Zedler 1977). Sprouting species on the other hand are at a distinct disadvantage the longer the fire-free period. The reasons are two-fold. One, during succession there is a constant thinning of shrubs. As the length of the fire-free period increases, shrub size increases so that individual shrubs appropriate a greater amount of space at the expense of neighboring shrubs. The result is a reduction in the density of potential resprouts. Second, as the stand of chaparral matures there is an accumulation of dead fuel which contributes to a more intense fire the older the stand of chaparral becomes. Thus, the longer the fire-free period the larger the openings after fire (fig. 2). This hypothesis suggests that occasional, long fire-free periods (e.g., 100 yrs or more) have been an important evolutionary stimulus for the obligate-seeding strategy.

What predictions can we deduce from this hypothesis? One prediction is that the abundance and diversity of obligate-seeding species should increase inversely in relation to the frequency of natural fires in the environment.

A TEST OF THE HYPOTHESIS

This is a very difficult prediction to test since the present temporal and spatial pattern of fire is man-made; e.g., in southern California man is responsible for nearly 99% of all acreage burned and he is also responsible for

extinguishing a great many lightning fires.^{4/} As an example, at the present time in southern California forests the equivalent of the total acreage of these forests is burned by man ca. once every 50 yrs; by lightning it's once every 4000 yrs. Suffice it to say we do not know what the natural pattern of fire is in chaparral. To even approach this goal would require a large scale modeling effort (e.g., Hobbs 1974).

However, there are data available on the frequency and distribution of lightning fires in chaparral regions. Although the number of lightning fires is not a definitive measure of the natural fire frequency it at least tells us something about the relative spatial pattern of natural fires. Explicitly this assumes that a lightning fire in one location is equivalent to one in another area. This certainly will not be the case, due to variations in burning conditions, but it should provide a reasonable first approximation.

Data from Court (1960) and Komarek (1967) provide an overview of lightning fire patterns in California. These data show three distinct patterns. Lightning fire frequency decreases

- 1) from northern to southern Calif. (fig. 3)
- 2) from medium-high to low elevation
- 3) from the interior to the coast

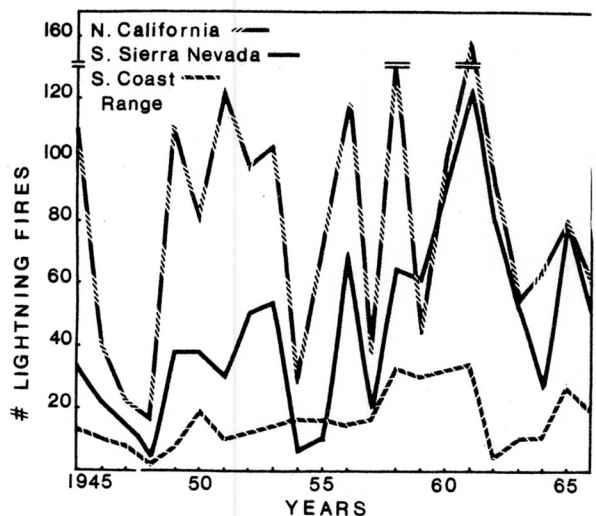


Figure 3--Lightning fires on National Forests of northern California, southern Sierra Nevada and southern Coast Ranges (from Komarek 1967).

^{4/} All fire statistics for southern California are from unpublished fire dispatcher data on statistical fires for the Los Padres, Angeles, San Bernardino (1965-1974), and Cleveland (1960-1974) National Forests.

Focusing on southern California we see these last two patterns repeated; a high correlation between # of lightning fires and elevation ($r_s = 0.71$, $P < 0.01$), and the more interior forests have higher frequencies than coastal ones.

Table 1--Lightning fire statistics for southern Calif. Nat. Forests (see footnote 4).

District	Mean Elevation		#/yr	ha/yr
	m	(ft)		
LP: Mt. Pinos	1700	(5800)	10.9	72
Santa Lucia	985	(3230)	1.9	11
Ojai	1620	(5340)	.9	2
Santa Barbara	975	(3200)	.6	9
Monterey	1615	(5300)	1.9	2
A: Valyermo	1890	(6190)	8.1	< 1
Mt. Baldy	1895	(6220)	2.2	2
Arroyo Seco	1490	(4880)	3.2	< 1
Tujunga	1520	(4990)	3.6	2
Saugus	1070	(3520)	.7	< 1
SB: San Jacinto	1795	(5890)	17.1	8
San Geronio	2665	(8740)	18.3	192
Big Bear	2145	(7130)	19.9	27
Arrowhead	1760	(5780)	6.9	< 1
Cajon	1850	(6070)	3.3	< 1
C: Palamar	1320	(4330)	7.3	158
Descanso	1220	(4000)	3.9	13
Trabuco	885	(2900)	.7	< 1

Based on these data there are two clear predictions. Comparing for example the Sierra Nevada and southern California, I would predict that 1) nonsprouting Ceanothus and Arctostaphylos would be most extensively developed (in diversity and abundance) in southern California and 2) within each region the abundance of nonsprouters would be highest at the lower elevations whereas the peak abundance of sprouters would be higher.

To test these predictions data was taken from Critchfield (1971); a compilation of > 10⁷ ha of line transects illustrating the dominant vegetation of California. From each of these vegetation profiles the length of transect occupied by sprouting and nonsprouting Ceanothus and Arctostaphylos was recorded (Table 2).

Table 2--Relative cover and # of species for Ceanothus and Arctostaphylos, by region.

	NONSPROUTERS		SPROUTERS	
	Transect (km)	# Sp.	Transect (km)	# Sp.
SIERRA NEVADA	265	7	274	6
SOUTHERN CALIFORNIA	868	25	333	7

There is certainly no question that the first prediction is upheld; the highest diversity

and greatest abundance of nonsprouting species is in southern California. The second prediction (fig. 4) is also confirmed. The abundance distribution of nonsprouting shrubs is centered around the lower elevations and the sprouting shrubs at the higher elevations. Thus, the region with the lowest lightning fire frequency is the southern coastal ranges; this is also the area which supports the greatest abundance and diversity of nonsprouting species. In contrast the mid-elevation range (2000 m) of the Sierras is a region with a very high lightning fire frequency and the chaparral of this area is quite depauperate in nonsprouting species.

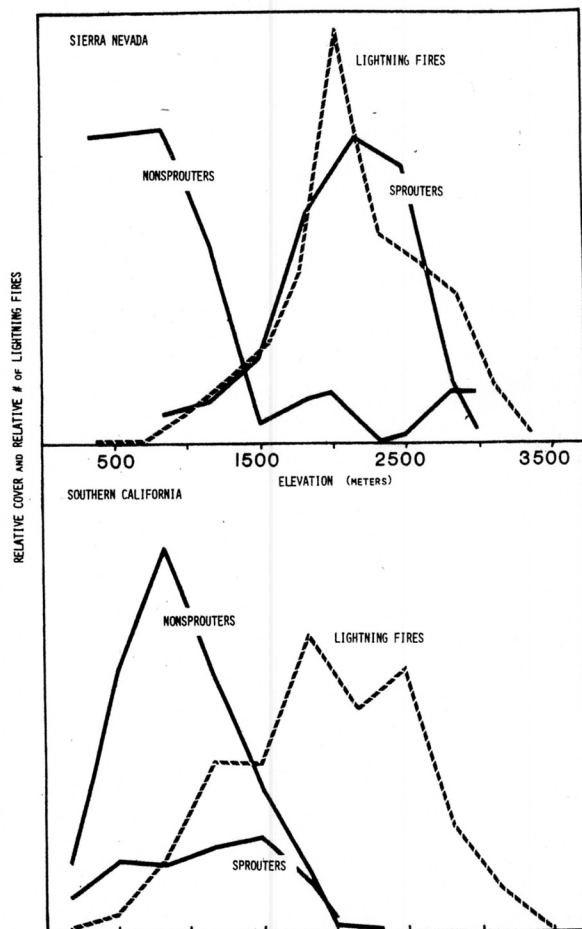


Figure 4--Relative shrub cover and relative # of lightning fires (Sierra Nevada lightning fire data from Komarek 1967).

One of the important conclusions from this hypothesis, particularly from a management perspective, is that the real selective pressure for the obligate-seeding strategy may have been the unpredictability (and consequently the occasional infrequency) of natural wildfires in the southern California chaparral. I would

envision an environment in which fire is inevitable but one in which, for any given patch of chaparral, there is a high probability of an occasional fire-free period for as long as a century or more.

Some may grimace at the thought of southern California chaparral having evolved under periodic long fire-free periods, however it is not an untenable hypothesis. Many of the coastal fire districts, which cover hundreds of thousands of hectares, have fewer than one lightning fire a yr. Generally these are accompanied by rain and it is likely that many would burn themselves out if given the chance. This is supported by the fact that there is a significantly greater # of lightning fires put out by the Cleveland National Forest Service today than 40 yrs ago ($\mu_{1935-1949} = 6.3/\text{yr}$ is less than $\mu_{1960-1974} = 11.9/\text{yr}$ by the Mann Whitney U-test, $P < .02$). I interpret this to mean that 40 yrs ago many lightning fires were allowed, knowingly or unknowingly, to burn themselves out and would do so today if given the chance.

A rejoinder to this argument would be that "a little fire can go a long way, particularly in chaparral." Witness for example the great fire holocausts such as burned much of San Diego Co. in 1970. These fires, however have two factors in common. Almost invariably they occur during Santa Ana (low humidity, high velocity foehn wind) conditions and they result from human ignition. It's questionable whether or not this sort of wildfire was a very frequent occurrence in the pre-hominid chaparral environment because lightning fires seldom occur even in the same month as Santa Ana conditions (fig. 5), let alone in concert with those conditions.

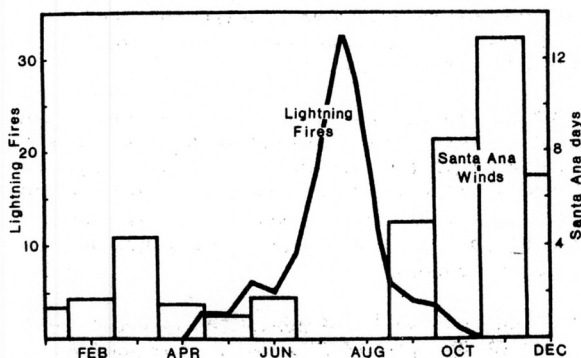


Figure 5--Monthly distribution of lightning fires and Santa Ana winds in southern California (10 yr ave). Santa Ana data from Weide (1968).

In conclusion, two caveats are in order. One is that the hypothesis for the origin of the obligate-seeding strategy is only one of

several tenable hypotheses; it is offered in that light. A second is that the arguments proposed here are not meant to play down the importance of fire in the chaparral environment, rather to emphasize the potential evolutionary importance of the unpredictability of fire in this environment. The management implications are manifold and certainly deserve future consideration.

LITERATURE CITED

- Axelrod, D. I.
1973. History of the mediterranean ecosystem in California, p. 225-277. IN F. diCasteri and H. A. Mooney (eds), Mediterranean type ecosystems: origin and structure. Ecological Studies Vol. 7. Springer-Verlag, N.Y.
- Court, A.
1960. Lightning fire incidence in northeastern California. USDA For. Ser. Tec. Pap. PSW-47.
- Critchfield, W. B.
1971. Profiles of California vegetation. USDA For. Ser. Res. Pap. PSW-76.
- Hobbs, J. A.
1974. Recreation, aesthetics, and the isomorphic fire regime, p. 195-200. IN M. Rosenthal (ed) Symposium on living with the chaparral. Sierra Club, San Francisco.
- Keeley, J. E., and P. H. Zedler.
1977. Reproduction of chaparral shrubs after fire: A comparison of the sprouting and seeding strategies. Am. Midl. Nat. IN PRESS.
- Komarek, E. V., Sr.
1967. The nature of lightning fires. Tall Timbers Fire Ecol. Conf., Proc. 7:5-41.
- Martin, P. S.
1973. The discovery of America. Science 179: 969-974.
- Raven, P. H.
1973. The evolution of mediterranean floras, p. 213-224. IN F. diCasteri and H. A. Mooney (eds), Mediterranean type ecosystems: origin and structure. Ecological Studies Vol. 7. Springer-Verlag, N.Y.
- Stebbins, G. L.
1974. Flowering plants: evolution above the species level. Harvard Univ. Press, Cambridge, Mass. 399 p.
- Weide, D. L.
1968. The geography of fire in the Santa Monica Mountains. M. S. Thesis. California State College, L. A. 183 p.
- Wells, P. V.
1969. The relation between mode of reproduction and extent of speciation in woody genera of the California chaparral. Evolution 23:264-267.